

VI. *Further Experiments upon the Blood Volume of Mammals and its Relation to the Surface Area of the Body.*

By GEORGES DREYER, M.A., M.D., *Professor of Pathology in the University of Oxford*, and WILLIAM RAY, M.B., B.Sc., *Philip Walker Student in Pathology in the University of Oxford.*

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(From the Department of Pathology, University of Oxford.)

In previous papers* we have shown that the blood volume of normal and healthy mammals, such as rabbits, guinea-pigs, and mice, is satisfactorily expressed by the formula $B = W^n/k$, where B is the blood volume in cubic centimetres, W the weight of the individual in grammes, n approximately $\frac{2}{3}$, and k a constant (calculated from the experiments), which varies with the particular species of animal. This formula indicates that the smaller and lighter animals of any given species, which have a relatively greater body surface than the heavier ones, have also a relatively greater blood volume—in other words, *the blood volume can be expressed as a function of the body surface*, and it must therefore be misleading to express it in per cent. of the body weight, since when so expressed it is not a constant for any given species of mammal.

As it was of interest to ascertain whether wild animals of closely allied species would differ greatly as regards their blood volume from the above-mentioned tame animals, we have determined the blood volume of hares, wild rabbits, and wild rats.

Technique.—The animals were used for the experiments immediately, or within a few days of capture. In the case of the hare and wild rabbit, the blood volume was determined by washing out the circulatory system with oxygenated Locke's fluid according to the method given in our last paper, and in the wild rat, by Welcker's method, modified as described in the same paper.

In all the tables, as in our previous paper, the weight of the animals is "Rohgewicht" in grammes, *i.e.*, the weight of the contents of the alimentary canal is not deducted: the blood volume is given in cubic centimetres, and the hæmoglobin is expressed as a percentage of the amount normal in man (man=100 per cent.).

In Table I are given the experimental results of the determination of the blood volume of five hares of weights varying from 2550 to 3780 grms., as well as

* *Vide* references at end.

the values for the blood constant k ($= W^{2/3}/B$), and the ratio of the blood volume to body weight expressed as a percentage of the latter.

TABLE I.

No.	Sex.	Body weight. ("Rohgewicht.")	Hæmoglobin per cent. (Man = 100.)	Blood volume observed.	Blood constant, k ($= W^{2/3}/B$).	Blood volume as percentage of body weight.
		grammes.		c.c.		
1	♂	2550	115.2	192.0	0.97	7.53
2	♂	2670	98.8	216.2	0.89	8.10
3	♂	2680	115.9	215.0	0.90	8.02
4	♂	2960	116.2	220.0	0.94	7.43
5	♂	3780	114.6	242.0	1.00	6.40
Average . . .			112.1	—	0.94	7.50

It is seen that the blood constant exhibits relatively small non-periodic deviations, and hence that, as shown in our previous communications, the lighter animals have a greater percentage of blood than the heavier ones. The average value of k is 0.94, and the average percentage 7.50.

TABLE II.

No.	Body weight. ("Rohgewicht.")	Blood volume observed.	Blood volume calculated. $B = W^{2/3}/k$. ($k = 0.94$.)	Difference between blood volume calculated and observed.	Blood volume calculated as per cent. (7.50) of body weight.	Difference between blood volume calculated and observed.
	grammes.	c.c.	c.c.	per cent.	c.c.	per cent.
1	2550	192.0	198.6	3.32	191.2	0.42
2	2670	216.2	204.7	5.62	200.2	7.99
3	2680	215.0	205.2	4.78	201.0	6.97
4	2960	220.0	219.4	0.27	222.0	0.90
5	3780	242.0	258.1	6.24	283.0	14.49
Average . . .				4.05	—	6.15

In Table II it will be seen that the average deviation between the calculated and observed figures is only 4.05 per cent. if the blood volume is calculated as a function of the surface, while it is 6.15 per cent. when calculated as a percentage of the body weight.

In Tables III, IV, V, and VI are given the results of our experiments upon the blood volume of 11 wild rabbits, ranging in weight from 1195 to 1570 grms. In

Table III are given the blood volumes and the hæmoglobin percentages, as well as the blood constant $k (= W^{1/3}/B)$ and the blood volume expressed as percentage of body weight.

TABLE III.

No.	Sex.	Body weight. ("Rohgewicht.")	Hæmoglobin per cent. (Man = 100.)	Blood volume observed.	Blood constant, $k (= W^{1/3}/B)$.	Blood volume as percentage of body weight.
		grammes.		c.c.		
1	♂	1195	93.0	54.8	2.05	4.59
2	♀	1350	89.6	56.0	2.18	4.15
3	♀	1350	81.2	61.0	2.00	4.52
4	♂	1390	75.3	64.0	1.95	4.60
5	♀	1440	83.0	64.5	1.98	4.48
6	♀	1450	80.6	61.9	2.07	4.27
7	♂	1480	94.7	67.0	1.94	4.53
8	♀	1500	82.9	61.3	2.14	4.09
9	♂	1520	97.3	62.8	2.10	4.13
10	♀	1550	88.1	71.0	1.89	4.58
11	♂	1570	82.2	64.5	2.10	4.11
Average . . .			86.2	—	2.04	4.37

The average blood constant is 2.04, and the average percentage of blood to body weight is 4.37.

TABLE IV.

No.	Body weight. ("Rohgewicht.")	Blood volume observed.	Blood volume calculated. $B = W^{1/3}/k$. ($k = 2.04$).	Difference between blood volume calculated and observed.	Blood volume calculated as per cent. (4.37) of body weight.	Difference between blood volume calculated and observed.
	grammes.	c.c.	c.c.	per cent.	c.c.	per cent.
1	1195	54.8	55.2	0.72	52.2	4.98
2	1350	56.0	59.9	6.51	59.0	5.08
3	1350	61.0	59.9	1.84	59.0	3.39
4	1390	64.0	61.1	4.75	60.7	5.44
5	1440	64.5	62.5	3.20	62.9	2.54
6	1450	61.9	62.8	1.43	63.4	2.37
7	1480	67.0	63.7	5.18	64.7	3.55
8	1500	61.3	64.2	4.52	65.5	6.41
9	1520	62.8	64.8	3.09	66.4	5.42
10	1550	71.0	65.7	8.07	67.7	4.87
11	1570	64.5	66.2	2.57	68.6	5.98
Average . . .				3.81	—	4.55

In Table IV the blood volume, as calculated from the average blood constant k (2.04), and from the average percentage (4.37), is given. It will be seen that the

average deviation between the calculated and observed figures in the former case is 3·81 per cent., while in the latter it is 4·55 per cent.

TABLE V.

Group.	Rabbits from Table III included in group.	Average body weight. ("Rohgewicht.")	Average blood volume observed.	Blood constant,* $k (= W^{1/3}/B)$.	Blood volume* expressed as percentage of body weight.
		grammes.	c.c.		c.c.
A	1	1195	54·8	2·05	4·59
B	2—4	1363	60·3	2·04	4·42
C	5—8	1468	63·7	2·03	4·34
D	9—11	1547	66·1	2·02	4·27
Average . . .				2·04	4·41

* The figures in these columns are calculated from the average body weight and the average blood volume of the group.

TABLE VI.

Group.	Rabbits from Table III included in group.	Average body weight. ("Rohgewicht.")	Average blood volume observed.	Blood volume calculated. $B = W^{1/3}/k$. (Average k for the groups, 2·04.)	Difference between blood volume calculated and observed.	Blood volume calculated as percentage of body weight. (Average for the groups, 4·41.)	Difference between blood volume calculated and observed.
		grammes.	c.c.	c.c.	per cent.	c.c.	per cent.
A	1	1195	54·8	55·2	0·72	52·7	4·74
B	2—4	1363	60·3	60·3	0·00	60·1	0·33
C	5—8	1468	63·7	63·3	0·63	64·7	1·55
D	9—11	1547	66·1	65·6	0·76	68·2	3·08
Average . . .					0·53	—	2·43

In Table V the experiments upon wild rabbits are arranged in four groups by averaging the weights and blood volumes of the animals in each group. The average blood constant is 2·04, while the average blood as percentage of body weight is 4·41. In Table VI is calculated the blood volume from the average blood constants of the groups (2·04), and from the average percentage (4·41) of the groups, and the percentage deviation between the calculated and observed values in each case is also given.

In the first case the deviation is only 0·53 per cent., whilst in the second it is 2·43 per cent. Here, as before, it is obvious that our formula represents the

experimental facts in a more satisfactory way than if the blood volume be calculated as percentage of the body weight, as has hitherto been usual.

In Tables VII, VIII, IX, and X are detailed the results of our experiments upon the blood volume of six wild rats, ranging in weight from 228 to 436 grms.

TABLE VII.

No.	Body weight. ("Rohgewicht.")	Hæmoglobin per cent. (Man = 100.)	Blood volume observed.	Blood constant, $k (= W^{\frac{2}{3}}/B)$.	Blood volume as percentage of body weight.
	grammes.		c.c.		
1	228	85.3	12.02	3.10	5.27
2	256	85.7	12.43	3.24	4.86
3	277	67.3	14.99	2.83	5.41
4	292	70.6	14.92	2.95	5.11
5	326	75.8	14.85	3.19	4.56
6	436	78.5	19.45	2.96	4.46
Average . . .		77.2	—	3.05	4.81

In Table VII are given the blood volumes and hæmoglobin percentages, as well as the values of the blood constant $k (= W^{\frac{2}{3}}/B)$, and the blood volumes expressed as percentage of the body weight. The average blood constant is 3.05, and the average percentage 4.81. It is seen, as usual, that although the blood constant varies only slightly and without periodicity, the ratio of blood volume to body weight decreases markedly, and more or less regularly, as the animals increase in weight.

TABLE VIII.

No.	Body weight. ("Rohgewicht.")	Blood volume observed.	Blood volume calculated. $B = W^{\frac{2}{3}}/k$. ($k = 3.05$.)	Difference between blood volume calculated and observed.	Blood volume calculated as per cent. (4.81) of body weight.	Difference between blood volume calculated and observed.
	grammes.	c.c.	c.c.	per cent.	c.c.	per cent.
1	228	12.02	12.24	1.80	10.97	9.57
2	256	12.43	13.22	5.98	12.31	0.97
3	277	14.99	13.93	7.61	13.32	12.54
4	292	14.92	14.43	3.40	14.04	6.27
5	326	14.85	15.53	4.38	15.68	5.29
6	436	19.45	18.86	3.13	20.97	7.25
Average . . .				4.38	—	6.98

Table VIII represents the blood volume calculated from the average blood constant (3.05), and from the average percentage (4.81). The average deviation between the

calculated and observed figures is, when calculated according to our formula, 4·38 per cent., whilst if calculated as percentage of body weight it is 6·98 per cent.

TABLE IX.

Group.	Rats from Table VII included in group.	Average body weight. ("Rohgewicht.")	Average blood volume observed.	Blood constant,* $k (= W^{\frac{1}{3}}/B)$.	Blood volume* expressed as percentage of body weight.
A	1	grammes. 228	c.c. 12·02	3·10	5·27
B	2 and 3	267	13·71	3·02	5·13
C	4 and 5	309	14·89	3·07	4·82
D	6	436	19·45	2·96	4·46
Average . . .				3·04	4·92

* The figures in these columns are calculated from the average body weight and average blood volume of the group.

In Table IX the rats are arranged in four groups according to weight, and the blood constant and blood percentage calculated from the average figures of these groups. Again it will be seen that while the constant varies slightly and without marked periodicity, the blood percentage falls regularly from 5·27 per cent. in the lightest group to 4·46 per cent. in the heaviest.

TABLE X.

Group.	Rats from Table VII included in group.	Average body weight. ("Rohgewicht.")	Average blood volume observed.	Blood volume calculated. $B = W^{\frac{1}{3}}/k$. (Average k for the groups, 3·04.)	Difference between blood volume calculated and observed.	Blood volume calculated as percentage of body weight. (Average for the groups, 4·92.)	Difference between blood volume calculated and observed.
A	1	grammes. 228	c.c. 12·02	c.c. 12·28	per cent. 2·12	c.c. 11·22	per cent. 7·13
B	2 and 3	267	13·71	13·64	0·51	13·14	4·34
C	4 and 5	309	14·89	15·03	0·93	15·20	2·04
D	6	436	19·45	18·92	2·80	21·45	9·32
Average . . .					1·59	—	5·71

In Table X the blood volume is calculated from the average constant k of the groups (3·04), and from the average percentage of the groups (4·92 per cent.). At the same time is given the percentage deviation between the calculated and

observed figures in each case. The average percentage deviation between the calculated and observed figures is 1·59 per cent. if the blood volume be calculated according to our view, while it is 5·71 per cent. if expressed as percentage of the body weight.

Our experiments upon *freshly-caught normal and healthy mammals* which have lived in a natural state, such as hares, wild rabbits, and wild rats, therefore prove as clearly as did our experiments upon the tame rabbit, guinea-pig, and mouse, that our formula $B = W^{\frac{2}{3}}/k$ (indicating that the blood volume is a function of the surface) holds good, and represents the experimental facts in an extremely satisfactory manner. At the same time it is obvious from these experiments that the blood volume as percentage of body weight is, in any given species of the animals investigated, anything but a constant, and that any attempt to express it as such must be misleading and tend to obscure an important truth.

TABLE XI.

Species.	Range of weight. ("Rohgewicht.")	Average difference between blood volume calculated and observed. $B = W^{\frac{2}{3}}/k$.	Average difference between blood volume calculated and observed. $B =$ per cent. body weight.	Heaviest animal in terms of the lightest.	Difference according to weight in terms of difference according to surface.
	grammes.	per cent.	per cent.		
Tame rabbit	670—3250	4·61	9·11	4·85	1·90
Guinea-pig .	215—825	4·57	9·27	3·84	2·03
Mouse . . .	11·90—29·35	6·65	8·61	2·47	1·29
Hare . . .	2550—3780	4·05	6·15	1·48	1·52
Wild rabbit.	1195—1570	3·81	4·55	1·31	1·19
Wild rat. .	228—436	4·38	6·98	1·91	1·59
Average . . .		4·68	7·45	—	1·60

In Table XI are given the different species of animals upon which we have determined the blood volume, the range of their weights, and the average differences between the blood volume calculated, (*a*) as a function of the surface, and (*b*) as percentage of the body weight, and the observed figures. This table refers to the *individual* experiments, and the figures given have been calculated from the average *k* and from the average percentages of the *individuals* of each species. From this table it is clearly seen that in every case the average percentage difference between calculated and observed figures is much greater when the blood volume is calculated as percentage of the body weight than when calculated as a function of the surface. In the former case the average percentage difference between the calculated and the observed figures of the six species is 7·45 per cent., whilst in the latter it is only 4·68 per cent. At the same time it is seen that when the blood volume is calculated as percentage of body weight, the greater the range of weight of the animals

experimented upon the greater is the average difference between the calculated and observed values. This is not the case if the blood volume be calculated as a function of the surface.

As it is obvious that the percentage difference between the values calculated by the two methods and the values observed depends largely not only upon the actual range of weight of the animals, but also on the relative number of large and small animals, the actual difference between the two methods of calculation is brought out much more definitely by grouping together the animals of approximately the same weight within the same species.

TABLE XII.

Species.	Range of average weight of groups.	Average difference between blood volume calculated and observed. $B = W^{\frac{1}{k}}$.	Average difference between blood volume calculated and observed. $B = \text{per cent. body weight.}$	Heaviest group in terms of the lightest.	Difference in blood volume according to weight in terms of difference according to surface.
Tame rabbit	grammes. 670—3039	per cent. 2·77	per cent. 11·91	4·54	4·30
Guinea-pig .	245—825	1·92	10·87	3·37	5·66
Mouse . . .	12·94—25·84	1·35	6·38	2·00	4·73
Wild rabbit.	1195—1547	0·53	2·43	1·29	4·58
Wild rat. .	228—436	1·59	5·71	1·91	3·59
Average . . .		2·16	8·43	—	4·57

Accordingly in Table XII are given, for the different species, the average percentage deviations between the blood volumes calculated from the average blood constant for the groups and the average blood percentage of the groups for each species, and the observed values.

It is at once seen that if the blood volume be calculated as a function of the surface, the average percentage deviation is 2·16, whilst if it be calculated as percentage of body weight it is 8·43 per cent., or practically *four* times as great. At the same time it is seen that the greater the range of weight of the animals experimented upon the more misleading and erroneous it is to express the blood volume as a given percentage of the body weight.

The blood constants from which the blood volume of the normal healthy mammal can be calculated if the “Rohgewicht” of the animal is known, according to our formula $B = W^{\frac{1}{k}}$, are for the

Tame rabbit	1·58	Hare	0·94
Guinea-pig	3·30	Wild rabbit	2·04
Mouse	6·70	Wild rat	3·05

From these figures it is clear that a wild rabbit contains about 25 per cent. less blood in its circulatory system than a tame rabbit of exactly the same weight, while at the same time the percentage of hæmoglobin in its blood is nearly 25 per cent. more than in the tame variety. It is also interesting to note that if we compare a wild rabbit with a hare of the same weight, we find that the hare contains about 125 per cent. more blood, and that the percentage of hæmoglobin is about 30 per cent. greater.

As our experiments have shown that it is not only in animals constantly living in captivity, but also in animals of the same or closely allied species enjoying their natural life, that the blood volume is a function of the surface, it is interesting to ascertain if the blood volume continues to be a function of the surface under other conditions not interfering with the general health, but attended by a marked change in the blood volume, as, for example, in animals which have been transferred from a low to a high altitude.

Numerous and careful experiments upon the blood volume of rabbits at low and high altitudes have been carried out by E. ABDERHALDEN in his excellent work concerning the effects of high altitudes upon the number of red blood corpuscles, the percentage of hæmoglobin in the blood, and the blood volume, in tame rabbits.

We give below a brief account of ABDERHALDEN's results when dealt with according to our view.

Tables XIII–XX give ABDERHALDEN's results as to the blood volume of tame rabbits. The animals were derived from various stocks at Basle (266 metres above sea level) and transferred to St. Moritz (1856 metres above sea level), where, after four to eight and a half weeks, they were killed and their hæmoglobin percentage and blood volume determined.

Members of the same stock of animals remained in Basle to serve as controls, and a third group of members of the same stock were taken to St. Moritz, and after being kept there from four to eight weeks were brought back to Basle. Here their hæmoglobin percentage and blood volume were estimated after they had been back from 2 to 15 days.

Table XIII gives details of the weight, hæmoglobin percentage, and blood volume observed by ABDERHALDEN. From these data we have calculated the blood constant from the formula $k = W^{\frac{1}{3}}/B$, and the blood volume as percentage of the body weight in the animals killed at St. Moritz. The average blood constant is found to be 1.78, while the average figure representing the blood as percentage of body weight is 4.34. Here, again, it is seen that while the blood constant does not vary markedly according to the weight of the animal, the blood volume expressed as a percentage of body weight varies in the usual way, in that the smaller and lighter rabbits contain relatively more blood per unit of body weight than do the heavier ones.

TABLE XIII*.

No.	Reference in ABDER- HALDEN'S paper.	Sex.	Body weight. ("Rohgewicht.")	Blood volume observed.	Hæmoglobin (as given by ABDER- HALDEN).	Blood constant, $k (= W^{\frac{2}{3}}/B)$.	Blood volume as percentage of body weight.
			grammes.	c.c.			
1	X 2	♀	1200	60·3	13·41	1·87	5·03
2	IX 6	♀	1620	81·0	13·81	1·70	5·00
3	XI 1	♀	1649	76·3	14·22	1·83	4·63
4	XI 2	♀	1710	76·2	14·77	1·87	4·46
5	III 4	♀	1928	88·8	14·05	1·74	4·61
6	VII 7	♀	2120	88·8	14·87	1·86	4·19
7	VII 3	♀	2120	98·1	12·96	1·68	4·63
8	VI 4	♀	2170	87·8	15·32	1·91	4·05
9	VI 2	♀	2175	113·9	15·77	1·47	5·24
10	IX 5	♀	2215	97·6	14·71	1·74	4·54
11	VIII 1	♀	2457	89·8	15·41	2·03	3·65
12	IV 6	♀	2609	113·8	16·12	1·66	4·36
13	VIII 7	♀	2615	87·1	16·22	2·18	3·33
14	III 1	♀	2641	121·6	14·56	1·57	4·60
15	IV 4	♀	2715	103·2	15·22	1·88	3·80
16	II 2	♀	2840	124·2	14·29	1·62	4·37
17	V 6	♀	2875	112·2	14·45	1·80	3·90
18	V 2	♀	2900	116·8	14·09	1·74	4·03
19	II 6	♀	3112	124·5	14·92	1·71	4·00
Average . . .					14·69	1·78	4·34

* ABDERHALDEN'S experimental data are printed in light type. The figures calculated by us are printed in heavy type.

In Table XIV we have calculated the blood volume from the average blood constant (1·78), and from the average percentage (4·34). At the same time, the difference between the calculated and observed figures is given in per cent. according to the two methods. The average percentage deviation is seen to be 7·01 per cent., if the blood volume be calculated as a function of the surface, while it is 8·21 per cent. if it be calculated as percentage of body weight.

In Table XV we have arranged the animals in four groups according to their weights, giving a range in weight from 1545 to 2888 grms., and the average blood volumes of the groups. There is also given the blood constant $k (= W^{\frac{2}{3}}/B)$, and the blood volume as percentage of body weight. Here, again, it is seen that the blood constant does not vary greatly as the groups increase in weight, although the percentage of blood to body weight decreases regularly from 4·92 to 4·02 per cent.

In Table XVI is calculated the blood volume, from the average blood constant of the groups (1·76), and also from the blood as percentage of body weight (percentage = 4·39). There are also shown the percentage differences between the

TABLE XIV*.

No.	Reference in ABDER- HALDEN'S paper.		Sex.	Body weight. ("Rohgewicht.")	Blood volume observed.	Blood volume calculated. $B = W^{3/4}/k$ ($k = 1.78$.)	Difference between blood volume calculated and observed.	Blood volume calculated as per cent. (4.34) of body weight.	Difference between blood volume calculated and observed.
				grammes.	c.c.	c.c.	per cent.	c.c.	per cent.
1	X	2	♀	1200	60.3	63.4	4.89	52.1	15.78
2	IX	6	♀	1620	81.0	77.6	4.38	70.3	15.21
3	XI	1	♀	1649	76.3	78.5	2.80	71.6	6.56
4	XI	2	♀	1710	76.2	80.3	5.10	74.2	2.69
5	III	4	♀	1928	88.8	87.1	1.95	83.7	6.09
6	VII	7	♀	2120	88.8	92.8	4.31	92.0	3.48
7	VII	3	♀	2120	98.1	92.8	5.71	92.0	6.63
8	VI	4	♀	2170	87.8	94.1	6.70	94.2	6.79
9	VI	2	♀	2175	113.9	94.2	20.90	94.4	20.64
10	IX	5	♀	2215	97.6	95.3	2.42	96.1	1.56
11	VIII	1	♀	2457	89.8	102.3	12.21	106.6	15.78
12	IV	6	♀	2609	113.8	106.3	7.06	113.2	0.53
13	VIII	7	♀	2615	87.1	106.4	18.12	113.5	23.24
14	III	1	♀	2641	121.6	107.3	13.32	114.6	6.11
15	IV	4	♀	2715	103.2	109.3	5.58	117.8	12.41
16	II	2	♀	2840	124.2	112.5	10.40	123.3	0.73
17	V	6	♀	2875	112.2	113.6	1.23	124.8	10.20
18	V	2	♂	2900	116.8	114.2	2.28	125.9	7.23
19	II	6	♀	3112	124.5	119.8	3.92	135.1	7.85
Average . . .							7.01	—	8.21

* ABDERHALDEN'S experimental data are printed in light type. The figures calculated by us are printed in heavy type.

TABLE XV*.

Group.	Rabbits from Table XIII included in group.	Average body weight. ("Rohgewicht.")	Average blood volume observed.	Blood constant,† $k (= W^{3/4}/B)$.	Blood volume† expressed as percentage of body weight.
A	1—4	grammes. 1545	c.c. 76.0	1.76	4.92
B	5—9	2103	95.5	1.72	4.54
C	10—14	2507	102.0	1.81	4.07
D	15—19	2888	116.2	1.74	4.02
Average . . .				1.76	4.39

* ABDERHALDEN'S experimental data are printed in light type. The figures calculated by us are printed in heavy type.

† The figures in these columns are calculated from the average body weight and the average blood volume of the group.

TABLE XVI*.

Group.	Rabbits from Table XIII included in group.	Average body weight. ("Rohgewicht.")	Average blood volume observed.	Blood volume calculated, $B = W^{\frac{3}{4}}/k$. (Average k for the groups, 1.76.)	Difference between blood volume calculated and observed.	Blood volume calculated as per cent. (4.39) of body weight.	Difference between blood volume calculated and observed.
		grammes.	c.c.	c.c.	per cent.	c.c.	per cent.
A	1—4	1545	76.0	76.0	0.00	67.8	12.10
B	5—9	2103	95.5	98.9	3.44	92.3	3.47
C	10—14	2507	102.0	104.6	2.49	110.1	7.36
D	15—19	2888	116.2	115.4	0.69	126.8	8.36
Average . . .					1.66	—	7.82

* ABDERHALDEN's experimental data are printed in light type. The figures calculated by us are printed in heavy type.

figures calculated according to the two methods and the observed figures. Calculated as a function of the surface, the average percentage deviation of the blood volume is only 1.66 per cent., but if the blood volume be calculated as percentage of body weight, the average deviation between the calculated and observed figures is 7.82 per cent. In other words, the deviation on the latter plan of calculation is more than four times as great as when the blood volume is calculated as a function of the surface.

Tables XVII to XX deal with the results which ABDERHALDEN obtained upon the blood volume of rabbits which were taken from Basle to St. Moritz, and after living for from 4 to $8\frac{1}{2}$ weeks at the latter place were brought back to Basle. In these tables are included only those animals which were experimented upon after they had been back in Basle for three days or more.

In Table XVII are given the weights, blood volumes, and hæmoglobin percentages of the animals, and our calculations of the blood constants k ($= W^{\frac{3}{4}}/B$), and the blood volumes in percentages of body weight. The average blood constant is found to be 1.58, while the average blood percentage is 4.64 per cent.

In Table XVIII are calculated the blood volumes from the average blood constant (1.58), and from the average blood percentage (4.64), as well as the percentage difference between calculated and observed values in each case. Here, again, it will be seen that the average deviation is smaller when the blood volume is calculated according to our formula (6.00 per cent.) than if calculated as percentage of the body weight (6.49 per cent.).

To bring out more convincingly the real differences shown by the two methods of calculation, we have arranged the animals in four groups in Table XIX, and the

TABLE XVII*.

No.	Reference in ABDER- HALDEN'S paper.	Sex.	Body weight. ("Rohgewicht.")	Blood volume observed.	Hæmoglobin (as given by ABDER- HALDEN).	Blood constant, $k (= W^{1/3}/B)$.	Blood volume as percentage of body weight.
			grammes.	c.c.			
1	XI 3	♀	1815	89.2	12.23	1.67	4.92
2	X 8	♂	1895	89.3	13.01	1.71	4.71
3	IV 1	♂	2175	115.6	11.61	1.46	5.31
4	III 5	♀	2445	112.1	13.25	1.62	4.59
5	I 1	♀	2470	127.5	11.01	1.44	5.16
6	IX 7	♂	2514	111.6	12.64	1.65	4.44
7	VII 6	♀	2545	108.6	11.84	1.72	4.27
8	IX 1	♀	2705	114.0	11.76	1.70	4.20
9	VII 1	♂	2715	140.8	13.46	1.38	5.19
10	VIII 4	♂	2715	121.1	14.01	1.61	4.46
11	VI 3	♀	2855	125.3	13.21	1.61	4.39
12	I 4	♀	3025	145.5	13.64	1.44	4.81
13	VI 6	♂	3040	138.1	13.72	1.52	4.54
14	II 7	♀	3050	129.9	12.97	1.62	4.26
15	V 3	♀	3235	140.9	13.12	1.55	4.36
Average . . .					12.77	1.58	4.64

* ABDERHALDEN'S experimental data are printed in light type. The figures calculated by us are printed in heavy type.

TABLE XVIII*.

No.	Reference in ABDER- HALDEN'S paper.	Sex.	Body weight. ("Rohgewicht.")	Blood volume observed.	Blood volume calculated. $B = W^{1/3}/k$ ($k = 1.58$)	Difference between blood volume calculated and observed.	Blood volume calculated as per cent. (4.64) of body weight.	Difference between blood volume calculated and observed.
			grammes.	c.c.	c.c.	per cent.	c.c.	per cent.
1	XI 3	♀	1815	89.2	94.1	5.21	84.2	5.94
2	X 8	♂	1895	89.3	97.0	7.94	87.9	1.59
3	IV 1	♂	2175	115.6	106.2	8.85	100.9	14.58
4	III 5	♀	2445	112.1	114.8	2.35	113.5	1.23
5	I 1	♀	2470	127.5	115.9	10.00	114.6	11.28
6	IX 7	♂	2514	111.6	116.8	4.46	116.6	4.29
7	VII 6	♀	2545	108.6	118.0	7.96	118.1	8.05
8	IX 1	♀	2705	114.0	122.8	7.16	125.5	9.16
9	VII 1	♂	2715	140.8	123.4	14.10	126.0	11.74
10	VIII 4	♂	2715	121.1	123.4	1.86	126.0	3.89
11	VI 3	♀	2855	125.3	127.5	1.73	132.5	5.44
12	I 4	♀	3025	145.5	132.3	9.96	140.4	3.64
13	VI 6	♂	3040	138.1	132.7	4.07	141.1	2.13
14	II 7	♀	3050	129.9	133.2	2.48	141.5	8.20
15	V 3	♀	3235	140.9	138.3	1.88	150.1	6.13
Average . . .						6.00	—	6.49

* ABDERHALDEN'S experimental data are printed in light type. The figures calculated by us are printed in heavy type.

blood constant, and blood volume as percentage of body weight, are calculated from the average figures of the groups.

TABLE XIX*.

Group.	Rabbits from Table XVII included in group.	Average body weight. ("Rohgewicht.")	Average blood volume observed.	Blood constant,† $k (= W\frac{1}{2}/B)$.	Blood volume† expressed as percentage of body weight.
		grammes.	c.c.		
A	1—3	1962	98·0	1·60	4·99
B	4—7	2494	115·0	1·60	4·61
C	8—11	2748	125·3	1·57	4·56
D	12—15	3088	138·6	1·53	4·49
Average . . .				1·58	4·66

* ABDERHALDEN'S experimental data are printed in light type. The figures calculated by us are printed in heavy type.

† The figures in these columns are calculated from the average body weight and the average blood volume of the group.

The average blood constant of the groups is 1·58, and the average blood percentage is 4·66 per cent. Here, again, there is a regular decrease in the blood as percentage of body weight as the animals increase in weight.

TABLE XX*.

Group.	Rabbits from Table XVII included in group.	Average body weight. ("Rohgewicht.")	Average blood volume observed.	Blood volume calculated. $B = W\frac{1}{2}/k$. (Average k for the groups, 1·58.)	Difference between blood volume calculated and observed.	Blood volume calculated as percentage of body weight. (Average for the groups, 4·66.)	Difference between blood volume calculated and observed.
		grammes.	c.c.	c.c.	per cent.	c.c.	per cent.
A	1—3	1962	98·0	99·1	1·11	91·4	7·23
B	4—7	2494	115·0	116·4	1·20	116·2	1·03
C	8—11	2748	125·3	124·2	0·89	128·1	2·18
D	12—15	3088	138·6	134·2	3·28	143·9	3·68
Average . . .					1·62	—	3·51

* ABDERHALDEN'S experimental data are printed in light type. The figures calculated by us are printed in heavy type.

In Table XX are calculated the blood volumes from the average blood constant of the groups (1·58), and from the average blood percentage of the groups (4·66 per

cent.). The percentage deviation between the calculated and observed figures is, in the two cases, 1.62 and 3.51 per cent. It will be seen that the average percentage deviation between the calculated and observed figures is, as usual, much greater when the blood volume is calculated as percentage of body weight than when it is calculated as a function of the surface.

If the average blood constant is calculated from the great number of rabbits which were kept at Basle as controls, it will be found to be 1.60, and the blood volume expressed as per cent. of body weight to be 4.64 per cent.

If we compare ABDERHALDEN's results on rabbits which were kept as controls at Basle with those on rabbits which were brought back to Basle after having been at St. Moritz, it will be found that they have practically the same blood constant in the two cases (1.60 and 1.58). Hence, it appears that after three days in Basle, the rabbits which had been at St. Moritz had regained the same blood volume as the control animals.

There is, therefore, complete and striking agreement between the results which ABDERHALDEN obtained on his great number of Basle rabbits and the results which we published in our last paper, the blood constant $k (= W^{2/3}/B)$ being practically identical in both cases—in the case of ABDERHALDEN's two sets of Basle rabbits 1.60 and 1.58 respectively, and in the case of our own 1.58, a difference of about 0.60 per cent.

ABDERHALDEN's results are, it will be noticed, entirely different, as were our own, from the results obtained on rabbits by DOUGLAS and by BOYCOTT and DOUGLAS (using the CO method as employed by HALDANE and LORRAIN SMITH), in that they find a much larger blood volume, the average blood constant calculated from their experiments being 1.40, and the blood volume expressed as a percentage of body weight 5.27 per cent. Comparing this with ABDERHALDEN's constant (1.59) and blood percentage (4.64 per cent.), it is seen that they find about 13 per cent. more blood than either ABDERHALDEN or ourselves, and that this is the case whether the blood volume be calculated as a function of the surface or as a percentage of the body weight.

It is further to be seen from ABDERHALDEN's experiments that there is no definite difference in the blood volume of males and females, the average blood constant being practically the same in both sexes. This is in agreement with the results (already published) of our own experiments, pregnant animals being, of course, excluded.

In our last paper we drew attention to the fact that the power $\frac{2}{3}$ in our formula for the blood volume was only approximately correct. This is shown by the fact that if the animals be grouped together the constant shows a tendency towards a slight increase in the light-weight groups compared with its size in the heavy-weight groups when the weights of the animals cover a sufficiently large range. At the same time we pointed out that if the body surface be calculated from the body weight according to MEEH's formula ($S = k \cdot W^{2/3}$) the power $\frac{2}{3}$ in this case is only

approximately correct also, as here, too, the constant k in this formula shows a tendency to be slightly smaller in the lighter animals than in the heavier ones. In both cases, as we have already pointed out, the slight periodical change disappears if the power $\frac{2}{3}$ be replaced by a slightly greater one (0.71–0.72). At the same time we also pointed out that the power $\frac{2}{3}$ is sufficiently accurate for all practical purposes and was adopted by us as being much more convenient for calculation.

To make clear the influence of slightly increasing the power $\frac{2}{3}$ in calculating the *surface* we have introduced Tables XXI, XXII, and XXIII.

TABLE XXI*.

Group.	Subjects from MEEH'S table included in group.	Average body weight. ("Rohgewicht.")	Average body surface.	Surface calculated. $S = W^n \cdot k$. $n = \frac{2}{3}$. $k = 12.23$.	Difference between surface calculated and observed.	Surface calculated. $S = W^n \cdot k'$. $n = 0.73$. $k' = 6.40$.	Difference between surface calculated and observed.	k . $(S = W^n \cdot k)$, where $n = \frac{2}{3}$.	k' . $(S = W^n \cdot k')$, where $n = 0.73$.
A	1—4	grammes. 8,224	sq. cms. 4,587.5	4,983	7.92	sq. cms. 4,615	0.59	11.26	6.36
B	5—8	20,966	9,311.0	9,298	0.14	9,139	1.88	12.25	6.52
C	11, 12, 13, 16	48,219	17,443.7	16,200	7.68	16,780	3.96	13.16	6.65
D	9, 10, 14, 15	66,375	20,067.8	20,040	0.14	21,190	5.30	12.24	6.06
Average . . .					3.97	—	2.94	12.23	6.40

* MEEH'S experimental data are printed in light type. The figures calculated by us are printed in heavy type.

In Table XXI, dealing with the experiments on the surface of man as measured by MEEH, the results obtained by this observer on 16 human beings weighing from 3020 grm. to 65,500 grm. are arranged in four groups by averaging the weights and surfaces of the members of each group. From the average weights and surfaces the two constants k and k' are calculated from the power n represented by $\frac{2}{3}$ and the "best n " 0.73, respectively ("best n " meaning here the power which for each species gives the smallest average percentage deviation between the calculated and observed figures). At the same time are calculated the percentage differences between the figures calculated with $n = \frac{2}{3}$ and $n = 0.73$, and the observed values. The average percentage deviation in the two cases is 3.97 per cent. and 2.94 per cent., which is a very marked improvement in the method of calculation and makes the result very nearly, and for all practical purposes, as good as if we introduce into the surface calculation, not only the weight, but also the length and girth, as has been done by MIWA and STOELTZNER. In this case the average percentage difference between the calculated and observed surfaces is 2.67 per cent. If the measurements on man be dealt with individually the "best n " reduces the average percentage difference between calculated and observed figures from 3.60 to 3.12 per cent.

In further illustration of this point are given in Tables XXII and XXIII the results of the determination of the surface of guinea-pigs and mice of greatly varying weight which have been made by us.

TABLE XXII.

No.	Body weight. ("Rohgewicht.")	Surface area observed.	Surface calculated $S = W^n.k$, $n = \frac{2}{3}$, $k = 9.56$.	Difference between surface calculated and observed.	Surface calculated. $S = W^n.k'$, $n = 0.72$, $k' = 7.03$.	Difference between surface calculated and observed.	k . ($S = W^n.k$), where $n = \frac{2}{3}$.	k' . ($S = W^n.k'$), where $n = 0.72$.
	grammes.	sq. cm.	sq. cm.	per cent.	sq. cm.	per cent.		
1	148	252	265.7	5.79	256.8	1.87	9.01	6.90
2	320	459	447.3	2.62	447.4	2.59	9.81	7.21
3	650	740	717.4	3.15	745.2	0.70	9.86	6.98
Average . . .			—	3.85	—	1.72	9.56	7.03

TABLE XXIII.

No.	Body weight. ("Rohgewicht.")	Surface area observed.	Surface calculated. $S = W^n.k$, $n = \frac{2}{3}$, $k = 10.50$.	Difference between surface calculated and observed.	Surface calculated. $S = W^n.k'$, $n = 0.69$, $k' = 9.86$.	Difference between surface calculated and observed.	k . ($S = W^n.k$), where $n = \frac{2}{3}$.	k' . ($S = W^n.k'$), where $n = 0.69$.
	grammes.	sq. cm.	sq. cm.	per cent.	sq. cm.	per cent.		
1	10.66	50.5	50.37	0.26	50.48	0.04	10.42	9.87
2	17.46	71.0	70.66	0.48	70.94	0.08	10.55	9.87
3	19.73	77.0	76.68	0.42	77.20	0.26	10.54	9.84
Average . . .			—	0.39	—	0.13	10.50	9.86

The weight, as usual, means "Rohgewicht" in grammes, and the surfaces were determined by carefully skinning the animals, making accurate drawings of the skin and determining the surface thus marked out both by planimeter and by the weight of the cut out area of paper, both methods giving the same results. In both Tables XXII and XXIII it will be seen, as in the case of man, that if the power $\frac{2}{3}$ be used the constant k gradually increases as the animals increase in weight, whilst this is not the case if the best n (being in the two cases 0.72 and 0.69) be chosen. Using the two different powers ($n = \frac{2}{3}$ and $n = \text{best } n$), the average percentage deviation between the calculated and observed figures is, in the case of the guinea-pig, 3.85 per cent. and 1.72 per cent. respectively, while in the case of the mouse it

is 0·39 per cent. and 0·13 per cent. It is to be noted further that the average best n in the three species is between 0·71 and 0·72, exactly as will be seen when the best n for the blood volume is determined.

Having shown the effect of slightly increasing the size of “ n ” in the case of MEEH’s formula, we will return to our own experiments upon the blood volume, and show the similar effect of slightly increasing the power $n (= \frac{2}{3})$ in the formula for calculating the blood volume ($B = W^n/k$).

TABLE XXIV.

Animal.	Best n .	Average percentage deviation with			Constants.	
		$n = \frac{2}{3}$.	Best n .	Percentage, body weight.	$n = \frac{2}{3}$.	Best n .
Rabbit, tame	0·72	4·61	4·50	9·11	1·58	2·37
Guinea-pig	0·71*	4·57	4·28*	9·27	3·30	4·28
Mouse	0·72	6·65	6·32	8·61	6·70	7·85
Hare	0·63	4·05	3·78	6·15	0·94	0·70
Rabbit, wild	0·72	3·81	3·81	4·55	2·04	3·00
Rat, wild	0·72	4·38	3·88	6·98	3·05	4·13
Average		4·68	4·43	7·45	—	—

* With $n = 0·72$ the deviation is 4·33 per cent. and the constant 4·55.

In Table XXIV are given the average percentage deviations (for the individual observations within each species) between the figures calculated when n is taken as $\frac{2}{3}$ and when the best n is used and the observed values. There is also appended the average percentage deviation for each species when the blood volume is calculated as percentage of body weight. As the value of k in the formula $k = W^n/B$ necessarily alters greatly with relatively small changes in the size of n , there is also given the value of k when $n = \frac{2}{3}$, and also for k when the “best n ” is used. From this table it will be seen, firstly, that the best n does not vary in the different species of animal, as it is in all cases practically the same (0·71 or 0·72), there being but one exception, the hare, where it is slightly less than $\frac{2}{3}$. No stress, however, can be laid upon this, as the observed animals of this species only cover a small range of weight. Secondly, it will be seen that in each species of animal the average percentage deviation between the calculated and observed blood volumes for the individual experiments is only slightly smaller in the case of “best n ” than it is in the case of $n = \frac{2}{3}$. The average percentage deviation of all the species is, for the best n , 4·43 per cent., and with $n = \frac{2}{3}$, 4·68 per cent. On the other hand there is a great difference if the blood volume be calculated as percentage of body weight, as here the average percentage deviation for all the species is 7·45 per cent.

Thus for all practical purposes, when *individual* animals are dealt with the

power $\frac{2}{3}$ is sufficiently accurate, as the best n (0.71 or 0.72) in this case only lessens the percentage deviation slightly.

If, however, we wish to bring out clearly from a theoretical point of view how much smaller the actual difference between calculated and observed values is when the blood volume is calculated as a function of the surface, compared with the percentage deviation when calculated as percentage of body weight, it is essential to make use of the power n which gives the best results when the animals are grouped according to their weight within each species, so as to reduce or eliminate the effect of individual errors as much as possible.

TABLE XXV.

Observer.	Species.	Best n .	Average percentage deviation with			Constants.		Heaviest group in terms of lightest.	Deviation by weight.	Deviation by weight.
			$n = \frac{2}{3}$.	Best n .	Percentage, body weight.	$n = \frac{2}{3}$.	Best n .		Deviation by $n = \frac{2}{3}$.	Deviation by best n .
DREYER and RAY . . .	Rabbit, tame	0.72	2.77	2.08	11.91	1.59	2.37	4.53	per cent. 4.30	per cent. 5.37
	Guinea-pig	0.71	1.92	0.91	10.87	3.29	4.28	3.37	5.66	11.96
	Mouse	0.71	1.35	1.06	6.38	6.68	7.36	2.00	4.73	6.02
	Rabbit, wild	0.72*	0.53	0.16*	2.43	2.04	3.00	1.29	4.59	15.20
	Rat, wild	0.72	1.59	0.92	5.71	3.04	4.12	1.91	3.59	6.20
RANKE . . .	Rabbit	0.72	4.79	3.72	13.92	2.55	3.64	4.72	2.77	3.58
ABDERHALDEN	Rabbit†	0.72	1.62	0.88	3.51	1.58	2.39	1.57	2.16	3.99
Average . . .			2.08	1.39	7.82	—	—	—	3.97	7.53

* With $n=0.73$ the deviation is 0.00 per cent., and k , 3.22.

† Refers to the experiments carried out at Basle on rabbits which had been at St. Moritz (see Tables XVII to XX).

Table XXV is similar in structure to Table XXIV, but refers to the *grouped* animals of each species, including our own experimental results as well as those of RANKE and ABDERHALDEN as calculated by us. Here again the best n is 0.71—0.72. The average percentage deviation between the calculated and observed figures is here smaller with the best n than it is with $n = \frac{2}{3}$, the average of the seven series of experiments being in the two cases 1.39 against 2.08 per cent. Note that the average percentage deviation for all the groups is 7.82 per cent. if calculated as per cent. of body weight.

We have found that the best n for the calculation of the surface by MEEH's formula ($S = k \cdot W^{\frac{2}{3}}$) in the mammal, taking man, guinea-pig, and mouse as examples, is not $\frac{2}{3}$, but, on an average, 0.71—0.72, exactly as is the case if the blood volume be calculated from the body weight according to our formula. It is therefore clear from the above table that the average percentage deviation between the calculated and observed figures for the above series of animals when the blood volume is calculated as percentage of body weight is from $5\frac{1}{2}$ to $7\frac{1}{2}$ times as great as it is when calculated as a function of the surface according to our formula, using the best n , and four times as large when n is taken $= \frac{2}{3}$.

For all experimental work, whether physiological, pharmacological, or pathological, where the blood volume is concerned, it is necessary to know, not only what the absolute blood volume is in normal animals of a given species, but also, what is equally important, the magnitude of the deviations from the average which may be met with in normal and healthy individuals, since otherwise it is impossible to decide whether the blood volume found by experiment is to be considered normal or abnormal. As we have now examined the blood volumes in a series of 72 mammals of six different species by a uniform and accurate procedure, we believe ourselves to be in a position to state what variations from the average may be met with in normal animals (*vide* Table XXVI).

TABLE XXVI.

Species.	Mean deviation ($n = \frac{2}{3}$).	Mean deviation (best n).
	per cent.	per cent.
Rabbit, tame	6.41	6.02
Guinea-pig	5.46	5.09
Mouse	9.03	8.91
Hare	5.11	4.73
Rabbit, wild	4.58	4.54
Rat, wild	5.24	5.11
Average	5.97	5.73

This table gives the *mean* deviations, as calculated by the method of least squares, for each of the six species of animals which we have examined, when the blood volume is expressed as a function of the surface ($B = W^{\frac{2}{3}}/k$). The average of the *mean* deviation for the six species is 5.97 per cent. if the power n is taken as $\frac{2}{3}$, and slightly smaller (5.73 per cent.) if the best n (0.71—0.72) is taken.

In Table XXVII we have given in percentages the cases in which the deviation falls within $\frac{1}{2}$, 1, $1\frac{1}{2}$, 2, 3, and 4 times the mean deviation, as well as the theoretical value of these percentages according to the law of the distribution of errors, using the method of least squares. It will be seen that, as regards the distribution of errors,

the agreement between the theoretical values and the values calculated from our experimental results is extremely good. It is therefore evident that it is justifiable to apply the method of least squares to our experimental results on the blood volume of mammals in order to calculate the *mean* deviation.

TABLE XXVII.

	Theoretical distribution. — Values.	Distribution found when $n = \frac{2}{3}$.	Distribution found when best n is used.
$\frac{1}{2}$ mean deviation . .	per cent. 38·3	per cent. 37·5	per cent. 40·2
1 " " . .	68·3	68·4	75·0
$1\frac{1}{2}$ " " . .	86·6	87·3	86·1
2 " " . .	95·4	95·8	95·8
3 " " . .	99·7	98·5	98·5
4 " " . .	99·994	100·0	100·0

As the *mean* deviation is about 6 per cent., this indicates that, if an individual animal is found by a reliable method to contain 12 per cent. more or less blood than it should if its blood volume were calculated from the surface, the average constant of the species being used, it is *probable* that the blood volume of the animal is abnormal, and, if it is 20 per cent. smaller or larger, it is *almost certain* that the blood volume is abnormally large or small. It may be pointed out, however, that if the blood volume were expressed as a percentage of body weight, it would only be possible to say with the same degree of certainty that the blood volume of an animal was abnormal, when it differed by at least 40 per cent. from the calculated figure.

Finally, it is of interest to point out that if the *mean* deviation for the hæmoglobin percentage be calculated for the same animals (which, of course, have lived under similar conditions), by the method of least squares, it is found to be 8 per cent. It is therefore evident, as we noted in our previous paper, that animals of the same species living under similar conditions vary less as regards their blood volume than they do as regards their hæmoglobin percentage.

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